PRELIMINARY NOTES ON THE ONTOGENY OF THE FRONTAL BODY WALL IN THE ADEONIDAE AND ADEONELLIDAE (BRYOZOA, CHEILOSTOMATA)

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ABSTRACT

Specimens of species belonging to 6 genera of the nominal family 'Adeonidae' have been found to exhibit two distinct forms of development of the calcified frontal body wall and the associated apparatus concerned with protrusion of the lophophore. The first type, found for example in *Adeona*, is interpreted as umbonuloid; the second, found in *Adeonella*, is interpreted as cryptocystidean. Both ontogenetic processes are briefly described, and some of the genera previously ascribed to the Adeonidae are provisionally placed together in the family Adeonellidae.

INTRODUCTION

The development of the calcified frontal body wall in the Cheilostomata and its relationships with the apparatus for protrusion of the lophophore have been discussed recently by Cheetham (1968), by Banta (1970, 1971) and by Tavener Smith & Williams (1970). Banta particularly considered some phylogenetic inferences resulting from his observations, and clarified and correlated much previous work, especially that of Silén (e.g. 1942) and Harmer (e.g. 1902, 1957). Both Cheetham and Banta introduced methods and defined criteria which may be applied to future studies affecting the taxonomy and classification of the Cheilostomata (*see also* Boardman & Cheetham 1969, Boardman *et al.* 1970). The observations made here, principally on a few members of one group, the 'Adeonidae', emphasize the fundamental nature of the problems which may be recognized as a result of this type of examination, and the wide scope for further study which has arisen from the most preliminary analysis.

The protrusion of the introverted lophophore in Bryozoa is effected by the increase in internal coelomic pressure as a result of muscular contraction. In

the Cheilostomata the type of calcification restricts the region available for muscular action to the area of the frontal body wall. In the Anasca, the frontal membrane is that part of the body wall delimiting the internal coleom frontally. Increase in internal pressure is accomplished by the contraction of the parietal muscles which are attached to the frontal membrane and extend to the basal or to the lateral walls. In the Cribrimorpha, the relationships are essentially the same, although the frontal membrane is variously overarched by a lattice of calcified spinous structures, leaving a space, the epistege, above it (*see* Banta 1970). In those Cheilostomata in which the frontal body wall is extensively calcified, two forms of apparatus for lophophore protrusion are known at present. In the first form, an anasciform frontal membrane and parietal muscles are present at an earlier ontogenetic stage than the calcification of the frontal body wall. In the second form, a sac-like proliferation of sub-opercular cells becomes attached to parietal muscles at a later stage than the primary calcification of the body wall. The correlation between the apparatus and the form and ontogeny of the calcification is not, however, a simple one. Much work remains to be done, including re-examination of specimens of the specific examples given by both Silén and by Harmer, as preliminary work has indicated that some of these may not, in fact, illustrate the relationships originally ascribed to them (*see* p. 260).

The genera considered here have usually been included in a single family, the Adeonidae (*see* Bassler, 1953 : G213 ; Harmer, 1957 : 788). With few exceptions they share an erect, branching bilaminar form of growth. They usually possess adventitious and vicarious avicularia, and have sexual polymorphs, those modified for brooding being of a distinct type. Most, but not all, possess a frontal pore, or complex of pores, here considered to be spiramina.

The family name Adeonidae was introduced by Jullien & Calvet (1903 : 53), as 'Adeonidae, J. Jullien, 1903'. Hincks (1887 : 150) had used the name several times (pp. 153, 155) in his discussion of Busk's family 'Adeoneae' (*see* Busk 1884 : 177), but had not introduced it formally as the name of a family. Both Hincks and Gregory (1893 : 241–244) made interesting observations on the heterogeneity of forms included in the family, especially noting the different types of development of the spiramina or frontal pores. Examination of species nominally classified within 6 genera of 'Adeonidae' showed that two major forms of development of the calcified frontal wall were present, and that two forms of protrusion apparatus could either be observed or inferred to be correlated with them. The genera have therefore been separated into two family groups, for convenience.

Adeonidae Jullien, 1903. Development of frontal wall umbonuloid (*see* p. 256). Operculum not sinuate. Marginal pores present. Frontal spiramina present, evanescent or permanent, single or multiporous. Avicularia with acute rostra usually present, adventitious and vicarious. Sexual polymorphs sometimes present, brooding internal.

Examples : *Adeona, Adeonellopsis, Reptadeonella, Bracebridgia.*

Adeonellidae Gregory, 1893. Development of frontal wall cryptocystidean (*see* p. 257). Primary calcified orifice and operculum sinuate. Marginal and usually frontal pores (pseudopores) present. Peristomial spiramina sometimes present.

Avicularia with acute and spathulate rostra usually present, adventitious and vicarious. Sexual polymorphs sometimes present, brooding internal.

Examples : *Adeonella, Laminopora.*

Many other genera, especially fossil examples, which have been placed in the 'Adeonidae', require investigation. Recently, some have been ascribed to other families (*see* p. 260 for summary).

Most of the specimens examined, from the collections of the British Museum (Natural History) (B.M.) and from the United States National Museum (U.S.N.M.) were in the dry state. Many very large, almost complete colonies in the British Museum were collected at least 90 years ago, and the growing edges were damaged and the surfaces covered with dirt. Detached pieces of these and whole specimens of the smaller colonies were soaked in 10 per cent trisodium phosphate solution for 24 hours, washed in water and gently cleaned in dilute detergent with a camel-hair brush, under a low-power microscope. This cleaned and restored much flexibility to the cuticular parts with little resulting damage. The specimens were examined in water after treatment, and differences in appearance noted when they were again dried. Similar comparisons were made between specimens preserved in alcohol and living colonies. Specimens of Adeonidae and Adeonellidae, together with some of species of Microporellidae, Inversiulidae and Umbonulidae, were also decalcified and sectioned. Some sections of *Reptadeonella* and *Escharoides* comprising soft and hard parts *in situ* were also examined. The ontogeny of frontal wall calcification has been directly observed in living specimens of *Reptadeonella.*

Specimens are referred to by the names and numbers under which they are currently stored. Many unnamed specimens of *Adeona* spp. at the British Museum (Natural History) together with MSS notebooks and drawings by Busk have been examined, but no attempt has been made to assign the material to described species, as a full study, particularly of the Australian reticulate forms, would first be necessary. Lack of suitable material has also restricted study of some forms ; for example, it was found impossible to prepare specimens of *Bracebridgia pyriformis* (the type-species of *Bracebridgia*) to show the ontogeny satisfactorily.

Terms used. Zooid is used for a unit of the colony, *autozooid* for an individual inferred or observed to have a feeding function. The term *sexual polymorph* is used for zooids which differ from the majority of autozooids in their calcified parts, and which may also be observed or inferred to have a sexual function, in some cases demonstrably as male individuals, in others as female brooding zooids. Much further work is needed to establish the kind and degree of sexual polymorphism occurring in the Adeonidae and Adeonellidae. The term *brooding zooid* is here used for sexually polymorphic zooids, which are usually enlarged in a lateral direction, and which have been observed, or can be inferred to have contained embryos.

The term *lophophore* includes tentacles and supporting structures, e.g. the tentacle sheath ; *ascus* refers to a sacciform structure derived from invagination of epidermal cells, and *ascopore* is restricted to a pore leading through both calcified and adjacent membranous layers into an ascus. The term ' *epistegal space* ' is used to denote the space above the frontal membrane in forms with umbonuloid development. It is analogous in function with an ascus, but developmentally similar in

its relationships to a cribrimorph epistege (*see* Larwood 1962). The term *spiramen* is here restricted to a pore leading through calcified tissues and adjacent membranous layers to a space which is morphologically frontal in position to the operculum (*see* p. 257).

OBSERVATIONS ON THE ADEONIDAE

1. *Reptadeonella violacea* (Johnston). *See* Harmer, 1957 : 814.

MATERIAL EXAMINED. B.M., living (later preserved dry and in alcohol), Ghana, Vernon Bank off Tema, 10 m, collected 1968, 1970 and 1972, registered as 1970.2.8.19, 1970.8.2.12 and 1972.1.2.11, respectively. In alcohol, English Channel, 1966.1.10.104 ; dry, Brazil, 1888.4.16.14–17.

Zoarium encrusting. Autozooids with a simple frontal spiramen and a distally or distal-laterally directed suboral avicularium. Vicarious avicularia absent. Some sexual polymorphs present which are larger than autozooids, with a wider secondary calcified orifice ; these have been observed to contain embryos and are brooding zooids. Male zooid polymorphs not recognized.

Primary zooidal development consists of two major episodes of rapid ontogenetic change, separated by a period of apparent quiescence. The edge of colonies in active growth consists of a zone of uncalcified buds, covered by distended, pale yellow cuticle. The calcification of basal, lateral and distal walls is rapid, and separate zooidal units are observable after 6–8 hours. Peripheral series of 2–4 rows of partially calcified zooids remain in this condition in the laboratory, with little apparent change for as long as 14 days. Under normal conditions this quiescent period may well be shorter, but the great majority of well-preserved colonies in the British Museum shows a zone of partially calcified zooids at the growing edge, and thus some pause in the calcification process seems to be usual. Primary calcification of the frontal body wall is extremely rapid and may be complete in less than 12 hours. Calcification commences as a thin lamina which is an inward extension of the proximal and lateral walls. The lamina advances distally and medially beneath the cuticle leaving regularly spaced uncalcified areas. These become the marginal pores at a later stage. In the central area of the membranous frontal wall the parietal muscles and, distally, the operculum are differentiated at this stage. The central part of the membrane then becomes depressed (probably as a result of the contraction of the parietal muscles), and the advancing calcified lamina can be seen to continue its development above the membrane, forming the ' epistegal space '. The developing lophophore can be seen beneath the membrane at this stage.

The membranous frontal body wall thus assumes the same relationship with the developing lophophore and viscera as does the frontal membrane in Anascan species, and the overarching calcified frontal shield assumes the same relationship with the frontal membrane as does the spinous frontal shield in the Cribrimorpha.

As calcification proceeds the tissues underlying the cuticle become brightly pigmented. The purple colour is at first concentrated around and above the

marginal pores; it spreads and darkens in later ontogenetic stages, and remains under the distended cuticle, even when the calcified layers beneath it have reached considerable thickness.

As the calcified lamina extends distally and medially over the frontal membrane, it develops paired, medially directed distal processes which meet and fuse centrally above the now fully functional operculum (*cf.* Pl. 1, figs. 1, 2). Thus a secondary, calcified orifice is formed. This differs from that of the cryptocystidean orifice of, for example, *Watersipora*, in that it is not in direct contact with, and does not exactly outline, the operculum, which is slightly below it. In *Watersipora* the primary orifice is calcified and is formed as a result of the contemporaneous differentiation of the operculum and the calcification of the surrounding membranous frontal body wall (*see* Banta 1970). In *Reptadeonella* the primary orifice is uncalcified and is formed by the opening of the operculum. The central foramen formed by the median fusion of the distal calcified processes (*see* Pl. 1, fig. 2) becomes reduced in size by further, centrally directed calcification, but remains open as a frontal spiramen. It is visible, even in zooids with considerably thickened frontal calcification, as a pit, lined with pigmented tissue beneath distended cuticle.

The lophophore and viscera are completely formed before the fusion of the distal processes, and the tentacles have been seen to be partially protruded at this stage. Generally the autozooids are feeding actively while the avicularian chamber is being formed, soon after the formation of the secondary calcified orifice. Brooding zooids have not been seen to protrude tentacles, nor have specifically male zooids been recognized. Thus many details of the degree and nature of sexual polymorphism are at present lacking.

Subsequent ontogenetic changes, although continuous, are apparently far slower than these primary episodes, and consist mainly of the thickening of frontal wall calcification and the development of secondary adventitious avicularia.

All these ontogenetic changes may be inferred in well-preserved material by observing zooids at various stages progressively from the growing edge towards the ancestrular region (*see* Boardman *et al.* 1970). In specimens preserved in alcohol, the primary membranous frontal body wall, the developing calcified lamina, the operculum and parietal muscles and the fusion forming the secondary calcified orifice can all be seen, although the cuticle is not as distended as in life. In dried specimens the cuticle covering the calcified lamina is shrunken and not easily visible, but the frontal membrane and operculum can be seen beneath the developing calcified frontal shield in some zooids.

2. *Adeona* sp. (Pl. 1, figs. 1–6).

Material examined. B.M., dry, ? Australia, 1934.2.10.8, and Port Jackson, Australia, 1886.5.26.1–4.

Zoarium erect, bilaminar and regularly reticulate, with round or oval fenestrae. Autozooids with a simple frontal spiramen and a median distal or distal-laterally directed avicularium proximal to the secondary calcified orifice. Vicarious avicularia rare. Fenestral kenozooids regularly present. Some polymorphic zooids

occurring in groups. These are large, with wider secondary calcified orifices than the autozooids, and are inferred to be brooding zooids ; separate male zooids not recognized.

At the growing edge there are zooids with basal lateral and distal calcified walls only, and with a shrunken membranous frontal wall. Proximally to these are autozooids with an incomplete curved calcified lamina, or a complete lamina, with a large central pore, beneath which the frontal membrane and operculum can be seen. Even more proximal zooids, at a later ontogenetic stage, show the development of the frontal avicularian chamber (*see* Pl. 1, figs. 4, 6). Scanning photographs show the distal median suture in the primary lamina, formed by the fusion of two distal lateral processes, as in *R. violacea* (*see* Pl. 1, fig. 3). They also show the progressive thickening of the calcified frontal shield, inferred from the increasing depth of smooth calcification lining the peristome, and the deepening of the pit formed around and above the frontal spiramen. The appearance of these specimens is very similar to that of dry specimens of *R. violacea,* and is inferred to represent a similar series of ontogenetic changes.

3. *Adeona foliacea* Lamouroux. *See* Harmer 1957 : 790.

Material examined. B.M., in alcohol and dry, Jedan, Aru Is., Siboga Stn. 273, 301A, 371A, 1972.10.1.2,1.

Zoarium erect, bilaminar, lobate, and articulated. Autozooids with a single frontal spiramen and a distal-laterally directed suboral avicularium. Vicarious avicularia frequent, marginal, little differentiated from the autozooids, with a frontal spiramen. Brooding zooids inferred to be the larger zooids of the lateral rows. Separate male zooids not recognized.

The earliest ontogenetic stages are not present, even in specimens preserved in alcohol. There are indications of a primary lamina in some broken zooids at the growing edge which suggests that the ontogeny resembled that of *Adeona* sp., above. The later stages, including the derivation of the median suboral avicularium chamber which is associated with paired lateral marginal pores, are the same as those seen in *Adeona* sp., above.

The large vicarious avicularia appear to develop in a similar manner to the autozooids, and have a frontal spiramen proximal to the rostrum. Unfortunately, none of the early stages in vicarious avicularian development has been preserved, and decalcified whole mounts show that there are no lophophores present in individuals at the later stages. Embryos have been seen in some of the submarginal zooids and these, at least, are therefore inferred to be brooding zooids.

4. *Adeonellopsis meandrina* (O'Donoghue & de Watteville) (Pl. 3, figs. 1–3). *See* O'Donoghue & de Watteville 1944 : 425, pl. 16, fig. 14.

Material examined. B.M., dry, Cape of Good Hope, 1840.9.30.29 ; Port Nolloth, South Africa, 1942.8.6.31 ; Lamberts Bay, South Africa, 1963.9.4.21 ; South Africa, 1968.1.16.125, 126.

Zoarium erect, bilaminar, foliaceous, convoluted and anastomosing. Autozooids with a simple frontal spiramen and paired medially directed lateral avicularia. Vicarious avicularia absent. Polymorphic zooids larger than autozooids, with wide secondary calcified orifices, inferred to be brooding zooids. Separate male zooids not recognized.

Stages in the development of the primary calcified lamina and frontal spiramen above the frontal membrane, like those in *R. violacea* and *Adeona* sp. above, have been seen. The development of the paired avicularia differs in that each chamber is derived separately from a marginal pore. In some zooids only one avicularium develops (*see* Pl. 3, fig. 3). Large polymorphic zooids are scattered in groups, and are inferred to be brooding zooids.

5. *Adeonellopsis* sp. (Pl. 2, figs. 1–3).

MATERIAL EXAMINED. B.M., dry, Broughton Island, Australia, 1883.11.29.55.

Zoarium (inferred from fragments) erect, with wide bilaminar, unbranched, crenulate and anastomosing laminae. Autozooids with a multiporous frontal spiramen, and a single median distal or distal-laterally directed avicularium. Vicarious avicularia large, scattered, directed distally. Brooding zooids inferred to be those larger than autozooids, with a larger multiporous frontal area.

The early ontogenetic stages in calcification of the primary lamina above the frontal membrane resemble those described above (*cf.* Pl. 1, fig. 4 with Pl. 2, fig. 1). After the fusion of the two processes in the distal part of the lamina, zooids at later stages differ in that the frontal spiramen calcifies as a large, porous plate. In the earliest stages finger-like processes protrude into the uncalcified central area. In later stages these fuse, forming a group of irregular pores. Further calcification consists of another series of processes which grow across the pores, producing a stellate effect. The smooth surface of the processes is similar to that of the calcification lining the peristome and the inner surface of the avicularian rostra. It contrasts strongly with the rounded blocks of calcification composing the frontal shield, as seen in frontal view (*see* Pl. 2, figs. 2, 3, and *see* Banta, 1971 : 168).

6. *Adeonellopsis* sp.

MATERIAL EXAMINED. U.S.N.M., dry, Australia.

Zoarium erect, bilaminar, branching. Autozooids with a single, stellate frontal spiramen and single or paired, distally directed suboral avicularia. Vicarious avicularia marginal. Sexual polymorphic zooids not recognized.

The earliest ontogenetic stages are rarely preserved, but appear to be similar to those of *A. yarraensis*, which this species strongly resembles. Use of the scanning electron microscope, however, has shown distinct differences in the mode of formation of the frontal spiramen. A pore is left as an uncalcified area as the frontal lamina grows distally, the calcification meeting distally beyond it. More proximally placed zooids show that as the frontal calcification thickens, the pore becomes sunken in a shallow pit, the sides of which are formed of smooth calcification. A series of finger-like processes grow medially from the sides of the pore,

at its basal level, i.e. below the secondarily thickened surface level of the frontal shield. Zooids at this stage of development also show paired grooves apparently associated with lateral marginal pores, which protrude into the proximal edge of the secondary calcified orifice, their edges producing a small sinus. Later development of the grooves in a frontal direction produces the suboral avicularian chambers. The interior of the rostra is lined with smooth calcification, which also extends into the secondary calcified orifice, filling the sinus and forming a shallow, curved projection, similar to that seen in *Bracebridgia subsulcata* (*see below*).

7. *Adeonellopsis yarraensis* (Waters). *See* Harmer 1957 : 799.

MATERIAL EXAMINED. B.M., dry, Uraga Channel, off Tokyo, Japan, 30C, 1972.9.1.1.

Zoarium erect, bilaminar and branching. Autozooids with a multiporous frontal spiramen and paired distal medially directed suboral avicularia. Vicarious avicularia rare, marginal and small, directed distally. Large submarginal polymorphic zooids present, inferred to be brooding zooids.

At the growing edge, the development of the proximal part of the curved lamina above the frontal membrane can be seen. Zooids more proximal in position show that the later ontogeny differs from that described above for other species. The lamina continues to grow distally, but does not produce large paired processes which fuse. At the distal edge it leaves a series of small shallow depressions, each with a central slit. Four or five of these are formed and, at the same stage, two medially directed grooves develop leading from the nearest lateral oral marginal pores on each side. The next stage appears to comprise general thickening of the calcification, deepening the grooves which begin to form avicularian chambers. The frontal shield is also extended distally beyond the avicularian chambers and the last developed depression. Concurrently, the depressions, which have become sunken in the surrounding calcification, produce finger-like processes from their walls which grow centrally to produce stellate pores. As calcification proceeds, the whole complex appears to migrate proximally, but this is an illusion related to the thickening of the frontal wall. The base and sides of the depressions are formed of smooth calcification, like that lining the peristome and avicularian rostra, and unlike that of the surrounding frontal shield.

8. *Adeonellopsis* sp.

MATERIAL EXAMINED. U.S.N.M., dry, 'Albatross' Stn. 2324, Havana, Cuba, 33 fathoms, Stn. 2336, 23°10′ N, 82°18′ W, 157 fathoms. B.M., dry, Discovery Bay, Jamaica, 200 feet, 1965.8.2.3, Havana, Cuba, 80 fathoms, 1911.10.1.1274, as *Porina subsulcata*.

Zoarium erect, bilaminar, branching. Autozooids with a simple frontal spiramen, and a distally directed suboral avicularium. Vicarious avicularia marginal. Sexual polymorphs not recognized.

This species closely resembles the specimen of *Porina subsulcata* illustrated by Smitt (1873, pl. 6, fig. 136). It may be distinguished from *Bracebridgia subsulcata*

(see below) by the constant presence of a simple frontal spiramen, by the distally directed, smaller suboral avicularium, and by the lack, in late ontogenetic stages of a raised ridge of calcification as in *B. subsulcata*. These closely similar species have been confused together, and the *Adeonellopsis* seems to be undescribed.

No zooids show the earliest stages of calcification; but a few have a simple lamina overarching a depressed frontal membrane. Two zooids show the development of the frontal spiramen from a notch in the distally advancing lamina. Later ontogenetic stages indicate that the avicularium is associated with one of the lateral marginal pores. The distal part of the peristome is at first raised, but becomes immersed as the calcification of the frontal shield thickens. Later stages include the development of small, variously orientated adventitious avicularia on the frontal.

9. *Bracebridgia subsulcata* (Smitt). (Pl. 2, figs. 4–6.) *See* Smitt, 1873 : 28, pl. 6, figs. 136–140.

Material examined. Naturhistoriska Riksmuseet, Stockholm, dry, types of *Porina subsulcata* Smitt, Florida, 35 fathoms, Pourtales Coll., no. 1837 (for figs. 136, 137) and no. 1829 (for figs. 138–140). U.S.N.M., dry, 'Albatross' Stn. 2405, 28°45′ N, 85°02′ W, 30 fathoms. B.M., dry, 13°50′ S, 38°46′ W, 32–38 fathoms, 1890.1.30.17–20; 'Challenger' Stn. 122, off Bahia, 1887.12.9.735a, 1934.2.16.42, as *Adeonella distoma* var. *imperforata* Busk (1884 : 188, pl. 20, fig. 4).

Zoarium erect, bilaminar, branching. Autozooids with no obvious frontal spiramen, but with a distal-laterally directed suboral avicularium, its rostrum protruding above the proximal edge of the secondary calcified orifice, which also has a small rounded projection. Vicarious avicularia marginal. Sexual polymorphic zooids not recognized.

Very few growing tips show zooids at the earliest stages of calcification of the frontal shield. In two zooids only, distal processes of the lamina can be seen to have fused distally to form a small pore (Pl. 2, fig. 4). In one of these zooids the ridge delineating the proximal edge of the avicularian chamber has been formed, and the frontal spiramen, just proximal to it, is nearly occluded (Pl. 2, fig. 5). All other zooids inferred to have reached the same or later ontogenetic stages have no sign of a spiramen, which is presumably completely closed by the development of the avicularium and the thickening of the calcification of the frontal shield (*see* Pl. 2, fig. 6). The periphery of the shield develops as a raised, pyriform ridge of calcification, the central part of the shield remaining relatively depressed (*see* Pl. 2, fig. 6). In later ontogenetic stages further thickening obscures the ridge, and small, variously orientated adventitious avicularia develop on the frontal.

Smitt's fig. 136 shows zooids with distinct simple frontal foramina. His figured specimen indicates that these are a representation of the depression between the two lateral ridges of calcification in the later ontogenetic stages.

Adeonellopsis distoma (Busk), *see also* Busk (1884 : 187, text-figs. 56, 57), is apparently not closely related to *A. distoma* var. *imperforata*. *A. distoma* has an extensive multiporous frontal spiramen.

1. *Adeonella coralliformis* O'Donoghue (Pl. 3, figs. 4–6). *See* O'Donoghue, 1924: 55, pl. 4, fig. 24.

MATERIAL EXAMINED. B.M., dry, South Africa, 1923.7.26.15, 1962.6.4.13; dry and in alcohol, South Africa, 1963.3.20.21, 1968.1.18.5.

Zoarium erect, bilaminar, branching. Autozooids with frontal pseudopores and marginal pores. Primary calcified orifice with a distinct rounded sinus. Secondary orifice raised, with paired lateral avicularia directed distally and medially. A bar extends above the orifice extending from each lateral flange of the peristome, forming a small secondary calcified orifice distally and a peristomial spiramen proximally. Vicarious avicularia small, marginal, variously orientated. Enlarged marginal zooids inferred to be brooding zooids.

This species is very similar in several characters to *A. regularis* Busk (1884: 186, text-fig. 55, pl. 20, fig. 2), also from South Africa, and a study of the variation of the two forms is necessary.

The specimens are well preserved and the growing tips are intact. Zooids at the edge have basal, lateral and distal walls calcified, the frontal wall being entirely membranous. Other zooids in the same horizontal series, or slightly proximal in position, show development of a thin porous lamina of calcification beneath the membrane. In a few zooids the calcification is incomplete, but in the majority has reached the distal end of the zooid. At this stage the outline of the operculum and primary orifice within the central, rounded, uncalcified area is visible. The next proximal zooids have a fully formed primary calcified orifice and operculum. It is not possible to see the development of an ascus in whole decalcified mounts, but the appearance of the young zooids is very similar to those of *Watersipora*, *Fenestrulina* and *Onchoporella*, in which the rapid growth of the ascus as a sac developing from an invagination of subopercular epidermal cells can be seen. It is therefore inferred that the development in *Adeonella* consists of calcification of a cryptocyst beneath a hypostegal coelom and frontal wall of cuticle and epidermis, as described in *Watersipora* by Banta (1970), and in *Schizoporella* by Banta (1971).

Scanning electron microscope photographs show that the proximal part of the orifice calcifies in two stages (*cf.* Pl. 3, figs. 4 and 5). Concurrently, paired lateral oral avicularian chambers are developed, apparently associated with marginal pores, but often showing frontal pseudopores at the bases of their cavities. More proximal zooids show a general thickening of the frontal calcification and the growth of a raised lateral peristome, which incorporates the developing avicularian rostra. Paired processes then grow medially from each lateral peristomial flange, which meet and fuse, forming a bar beneath which the proximal part of the primary calcified orifice is visible. Later ontogenetic stages consist of general thickening of the calcification, immersing the peristome, and producing an apparent migration of the peristomial spiramen proximally. In decalcified sections the relationships of the spiramen and operculum are visible, the retracted tentacles extending to the area behind the operculum.

2. *Adeonella polystomella* Reuss. *See* Cook 1968a : 180.

Material examined. B.M., in alcohol, 5°24′15″ N, off Ghana, 1926.12.7.9 ; 'Calypso' Stn. 1, 27°05′ N, 17°14′ W, 45–43 m, C 51 I, C 52 D, 1970.8.21 and 8 ; Marche-Marchad Coll., Senegal, 1970.7.8.21.

Zoarium erect, bilaminar, branching and occasionally anastomosing. Autozooids with marginal pores and only one series of frontal pores, and a sinuate primary calcified orifice. Paired suboral avicularia very small, directed distally. Vicarious avicularia rare, small, distally directed. Sexual polymorphic zooids probably present.

The earliest ontogenetic stages have not been preserved, but near the growing tips a few zooids show a partially calcified, rounded primary orifice. More proximal zooids show the development of the sinus and operculum. Scanning photographs indicate that the primary orifice is calcified in two stages, as in *A. coralliformis*.

The frontal calcification differs from other species examined in the absence of pseudopores from the central area. Specimen 1970.8.21.1 includes the extensive, encrusting base of a young colony, and these zooids show a single submarginal series of pseudopores. The small oral avicularia appear to develop directly from a pair of lateral marginal pores. The marginal zooids are slightly larger than those in the centre and may be sexual polymorphs, but it is not known whether they are male zooids, brooding zooids, or both.

3. *Laminopora bimunita* (Hincks). *See* Harmer 1957 : 820.

Material examined. B.M., dry, Port Elizabeth, South Africa, 1899.5.1.1346 ; East London, South Africa, 1942.8.6.32 ; Durban, South Africa, 1968.1.16.6 ; in alcohol, False Bay, South Africa, 1962.6.4.11.

Zoarium erect, bilaminar, broadly foliaceous. Autozooids with frontal and marginal pores and a distinctly sinuate primary calcified orifice. Paired avicularia with long, acute mandibles, placed at the level of the sinus and directed proximally and medially. Large, distally directed vicarious avicularia rare and scattered, not marginal. Large sexual polymorphic zooids present, some inferred to be brooding zooids.

The specimens from False Bay show development of a porous calcified lamina beneath a thick primary membranous layer, presumably consisting of cuticle and underlying epidermis and coelomic tissue. The avicularia develop in association with marginal pores and concurrently with the formation of the primary calcified orifice. No peristomial spiramen is formed in any of these specimens, although it has been reported to occur in this species (*see* Harmer 1957 : 821). Later calcification greatly thickens the frontal wall, the primary orifices becoming sunken at the bottom of pits.

Large zooids with a wide sinuate primary orifice and relatively small avicularia are present in 1968.1.16.61, either marginal in position or scattered in small groups throughout the colony. It is not known whether some of these zooids are males,

but, as Harmer described (1957 : 821), one type of large zooid has a narrow primary calcified orifice and sinus, the other, presumably the brooding zooid, has a wider primary calcified orifice with a shallow sinus.

4. *Laminopora contorta* Michelin, *see* Harmer 1957 : 819.

MATERIAL EXAMINED. B.M., dry, ? Cape St Vincent, 1854.11.15.334–336 (*see* Harmer 1957 *re* locality) ; in alcohol, ' Calypso ' Coll. Stn. 14, 14°53′43″ N, 23°31′24″ W, 25–30 m, 1970.8.2, 10, Stn. 26, 15°16′30″ N, 23°47′31″ W, 50–65 m, 1970.8.2.6, Stn. 75, 16°04′20″ N, 22°58′10″ W, 45 m, 1970.8.2.5 ; Marche-Marchad Coll., Senegal, 1970.8.2.22.

Zoarium erect, bilaminar, irregularly branching, occasionally anastomosing. Autozooids with frontal and marginal pores and narrow, distinctly sinuate primary calcified orifices. Avicularia, if present, small, acute, lateral, directed distally. Vicarious avicularia rare, marginal, small, directed distally. Sexual polymorphic zooids marginal or scattered, slightly larger than autozooids.

The frontal calcification is similar in appearance to that of *L. bimunita*. Zooids with an incompletely calcified primary orifice, and with a porous lamina beneath a thick brownish-purple membrane, are inferred to indicate cryptocystidean development. The external cuticular membrane is distended in specimens preserved in alcohol. As the frontal calcification thickens, the primary orifice becomes sunken in a pit, as in *L. bimunita* ; in neither species is a distinct, tubular peristome produced like that in *Adeonella*. Decalcified sections show the introverted lophophore with its tentacles extending up to the operculum and completely filling the space behind it. Scattered large zooids have a wider primary calcified orifice than that of the autozooids and are frequently without avicularia. They are inferred to be brooding zooids, although in view of the possible bisexual nature of similar zooids in *L. bimunita*, further work is needed to ascertain their function.

DEVELOPMENT IN THE ADEONIDAE AND ADEONELLIDAE

The developmental series in the species assigned to the genera *Reptadeonella*, *Adeona*, *Adeonellopsis* and *Bracebridgia* have in common the growth of a calcified lamina above a frontal membrane, in which both the parietal muscles and the operculum are differentiated and functional early in the zooidal ontogeny. This type of growth is similar to that found in *Umbonula*, *Escharoides*, *Metrarabdotos* and in some features in *Exechonella*, and is termed ' umbonuloid ' (*see* Cheetham 1968 : 58). Umbonuloid development has now been directly observed in living colonies of *Reptadeonella*, *Metrarabdotos* and *Exechonella*. In all three cases the early functioning of the parietal muscles, and their apparent contraction during development of the calcified frontal shield has been observed.

Umbonuloid growth may perhaps be regarded as the distal extension of a single layer of calcification from the gymnocyst above the frontal membrane. Theoretically this may be derived from a double-layered fold, in which the upper layer does not calcify. It is not known how nearly homologous this may be with some forms, at least, of Cribrimorph development, in which the gymnocystal extensions

are spinous or derived from spines and must, therefore, be double-layered. Some supporting evidence is provided by study of living specimens of *Reptadeonella* and *Metrarabdotos*, both of which have strongly pigmented coelomic tissues. The cuticle in both forms is transparent and in life heavily pigmented tissue is present above the calcified frontal shield and beneath the distended frontal cuticle. This tissue is concentrated around the marginal pores and is present beneath the cuticle of uncalcified marginal buds. It is therefore presumably associated with coelomic tissues and is strongly suggestive of the presence of a coelomic connection at least, probably through the marginal pores (*see* Banta 1971). Nutritive coelomic tissue is thus present in umbonuloid forms beneath the cuticle but above the frontal calcified layer in a position which is analogous, but not homologous, with the hypostegal coelom of the cryptocystidean forms. The relationships of the calcified layer and the protrusion apparatus in the members of the Adeonidae studied are, however, exactly the same as that found in the Cribrimorpha, and the ' epistegal space ' above the frontal membrane is analogous and may be homologous with an epistege. Thin sections of Ghanaian specimens of *Reptadeonella* comprising both soft and hard parts *in situ* and sections of decalcified species of other umbonuloid genera (including *Umbonula*, *Escharoides* and *Metrarabdotos*) show that cuticle and cellular tissues are sometimes present lining the upper side of the epistegal space formed by the basal side of the calcified frontal shield. As cuticle and presumably coelomic tissues are present on the frontal side of the shield as well, the supposition that the shield represents a partially calcified fold is well worth further investigation.

Umbonuloid development differs from that described as ' gymnocystidean ' (*see* Banta 1970 : 53), in that the calcified frontal shield is an extension from the gymnocyst above a membrane, not an extension of the gymnocyst itself at the expense of the frontal membranous area. This last would lead hypothetically to the formation of an ascus by invagination of subopercular cells of epidermal origin as in the ' cryptocystidean ' type of development.

The formation of the frontal pore or pore-complex differs entirely from that seen in species of Microporellidae, which apparently have cryptocystidean ontogeny. In whole decalcified mounts of these forms the development of the ascus can be seen, and in sections the ascopore can be seen to lead directly into the ascus. The frontal pore in the Adeonidae leads into the space above the frontal membrane, and, as it is in a position morphologically above the operculum, is a spiramen. It is here defined as a frontal spiramen, to distinguish it from the peristomial spiramen of the Adeonellidae (*see below*). Although the frontal spiramen complex may be large, especially in some of the sexual polymorphs of *Adeonellopsis*, it is not yet known whether it is significantly involved in the passage of water into the ' epistegal space ', during protrusion of the lophophore. Thin sections of *Adeona* show that the spiramen does not become occluded by calcification during the thickening of the frontal shield. Observations have been made on living *Metrarabdotos*, which has no frontal spiramen, but an elongated narrow peristome comparable with that of *Reptadeonella*. Protrusion in *Metrarabdotos* was generally quicker and more frequent than in *Reptadeonella*, but in neither species was there any noticeable difference in behaviour between them and cryptocystidean forms

with elongated peristomes, such as *Smittina remotorostrata* (Canu & Bassler), *see* Cook 1968a : pl. 8, fig. b, pl. 11, figs. c, d for general notes.

The later ontogenetic stages in the Adeonidae comprise the development of oral avicularia and the thickening of the frontal calcification. The single suboral, or paired, lateral-oral avicularia all appear to be derived in association with the marginal pores. Where the avicularium is single and median, as in many species of *Adeona* and *Adeonellopsis*, the chamber derives equally from both sides, a ridge forming suborally across the primary lamina distal to the frontal spiramen (*see* Pl. 1, fig. 4 ; Pl. 2, figs. 1 and 5). In *Bracebridgia*, only one lateral pore is involved. Concurrently, there is considerable thickening of the frontal calcification around the marginal pores and above the primary calcified lamina. The peristomial area also thickens frontally, although the peristome does not usually protrude above the general level of the frontal shield. In *Bracebridgia*, the distal part of the peristome is at first raised, but in later ontogenetic stages becomes immersed. The frontal spiramen becomes gradually obscured at the bottom of a pit in *Adeona* and *Adeonellopsis*, but in *Bracebridgia* is rapidly and completely occluded. In *Adeona* and *Adeonellopsis* in frontal view the position of the frontal spiramen appears to migrate proximally during ontogeny. Further calcification frequently occludes the frontal avicularia, and secondarily developed adventitious avicularia may be formed, with variable orientation, over the frontal shield.

There is evidence of a development series of increasing complexity in the ontogeny of the frontal spiramen, ranging from the single simple pore of *Adeonellopsis meandrina* to the multiporous complex of *A. yarraensis*. *Adeonellopsis* spp. nos. 5 and 6 above may show intermediate forms of development in the series, but further observations on other species are needed.

The developmental series in the species assigned to *Adeonella* and *Laminopora* is inferred to resemble that described as ' cryptocystidean ' (*see* Banta 1970). The frontal calcification consists of a distally advancing layer, with marginal pores and frontal pseudopores, beneath membranous layers with presumably an intervening hypostegal coelom. No muscles or operculum are fully differentiated until the outline of the primary orifice has been formed by the calcification. Once the operculum has been formed, the ascus is developed by an invagination of subopercular cells and the parietal muscles presumably develop in succession proximally as the ascus enlarges (*see* Harmer 1902).

In *Adeonella* the peristomial area becomes extended and thickened distally and laterally, and raised lateral oral avicularia are frequently formed. The lateral peristome then produces medially directed extensions which meet and fuse in the midline, forming a peristomial bar above the primary orifice. Further lengthening of the peristome by frontal thickening of calcification produces a narrow secondary orifice and a long suboral peristomial spiramen, which, like the frontal spiramen in the Adeonidae, may appear to migrate proximally during ontogeny. A peristomial spiramen formed from fused lateral oral processes is known in several genera of Bryozoa, for example, in *Gigantopora* (*see* Harmer 1957 : 879).

Further calcification may obscure the first formed avicularia, and secondary, adventitious avicularia, variously orientated, may be produced, resulting in an

appearance, in old, worn colonies, almost indistinguishable from specimens of *Adeona* at a similar ontogenetic stage.

Harmer (1957 : 805) considered that the ' ascopore ' of *Adeona* and the ' spiramen ' of *Adeonella* had fundamentally the same relationships. They both open into a space which is frontal in position in relation to the operculum, but differ entirely in structure, and in space and time relationships within the series of ontogenetic changes forming the calcified frontal body wall in the two families. Both types of spiramen differ from each other and from the ontogeny and relationships of the ascopore of the Microporellidae.

Banta (1970) has shown that conclusions drawn from examination of dried material, without comparison with well-preserved specimens showing the full ontogenetic series, are liable to be misleading. Where live specimens can be observed, and their appearance compared with those preserved in alcohol or as dry material, a sequence of inferences can be made with a fair degree of confidence. Banta has pointed out that the late ontogenetic stages in appearance of the cryptocystidean ascus and the umbonuloid equivalent are very similar.

Where a series of developing zooids is visible with a membrane which is left below the front of an advancing calcified lamina, and in which the operculum and parietal muscles are visible early in the ontogeny, umbonuloid development may be inferred. Comparison of stained whole mounts of growing edges of cryptocystidean species of *Watersipora*, *Stylopoma*, *Microporella* and *Onchoporella*, shows that the groups of cells producing the ascus take up stain differentially, and the developing ascus can be seen. This, together with other correlated observations, is taken to indicate cryptocystidean development.

In the absence of cuticle and epidermal layers, as for example in fossil material, it is at present impossible to do more than infer the course and type of calcification of the body wall by indirect means. Further investigations may provide more character correlations which will be recognizable in fossil specimens, and may lead to more confident inferences about their ontogeny (*see* Banta 1971 : 171). At present, for the Recent specimens studied, the following correlations may be suggested for those genera here assigned to the Adeonidae and to the Adeonellidae. Where members of a series of zooecia of increasing ontogenetic age can be inferred to develop a pore or pores in a primary lamina which has no pseudopores and which terminates in a non-sinuate, secondary, calcified orifice, and where the avicularian chamber or chambers are not associated with a raised lateral peristomial complex, the development is probably umbonuloid. Where members of a series of increasing ontogenetic age can be inferred to develop a porous lamina, terminating in a distinct, sinuate orifice and, in some cases, where a pore is produced by extensions from a raised peristomial avicularian complex, the development may be cryptocystidean.

DEVELOPMENT IN SOME OTHER FAMILIES

In the course of this investigation, specimens belonging to several other genera have been examined, notes made on the ontogenetic stages seen, and some types

of development inferred. Within the 'Adeonidae', many fossil genera remain to be examined. For example, the genera *Schizostomella* and *Dimorphocella* possess individuals with sinuate orifices and apparent frontal spiramina, together with polymorphic zooids, which may be inferred, by analogy, to have had a sexual function. The characters of these genera are urgently in need of investigation.

Several Recent genera, some including fossil species, have already been revised, and the following notes summarize the current position. *Inversiula* was referred to the Inversiulidae by Harmer (1957 : 955), but replaced in the Adeonidae by Powell (1967 : 339), on the grounds that Vigneaux's prior definition (1949 : 68) of the family stated that gonoecia (brooding zooids) were absent and that therefore *Inversiula* was excluded. *Inversiula* appears to develop in a typically cryptocystidean manner, the ascus forming from an invagination of a group of cells concurrently with the differentiation of the proximal opercular margin. The plane of the closed operculum, which is hinged distally, is nearly vertical to that of the frontal wall, and the distal wall is very shallow. In decalcified sections, the ascopore can be seen to communicate directly with the ascus, and is completely separate from the operculum and region of the tentacle sheath, in the same manner as that seen in *Fenestrulina* and *Onchoporella*, both members of the Microporellidae. Although modified brooding zooids have been described in one species of *Inversiula* by Powell (1967 : 340), this would appear to be an interesting case of convergence with the Adeonidae and the Adeonellidae, and I consider that *Inversiula* has closest relationships with the Microporellidae.

Triporula (synonym *Enantiosula*) and *Anarthropora* were referred to the Exechonellidae by Cook (1967 : 965), and inferred to have modified umbonuloid development.

The genera *Trigonopora* and *Metrarabdotos* were referred to the Umbonulidae and the Metrarabdotosidae respectively by Cheetham (1968 : 59, 62), who considered them both to have umbonuloid growth. The living specimens of *Metrarabdotos* observed have confirmed Cheetham's conclusions. Other umbonuloid genera mentioned by Cheetham, none of which, however, have been referred in the past to the 'Adeonidae', were *Umbonula*, *Hippopleurifera*, *Hippomenella* and *Posterula*, all placed by him in the Umbonulidae, and *Exochella* and *Escharoides* which he referred to the Exochellidae.

Some genera referred by Harmer (1957 : 651) to the Ascophora Imperfecta, and thus inferred by later workers to have umbonuloid development, do not appear to display this type of ontogeny of the frontal wall. Some preliminary observations on members of the Petraliidae, Petraliellidae and Celleporariidae indicate that their development is not umbonuloid, but may be similar to the cryptocystidean type.

CONCLUSIONS

At present there are alternative conclusions as to the composition and relationships of the families Adeonidae and Adeonellidae. First, the similarity in colonial structure and polymorphism may be considered to be such that the ontogeny of

the frontal shield and protrusion apparatus is not of phylogenetic significance. Second, it may be concluded that the groups are polyphyletic, exhibiting convergence between two or perhaps among several lines of evolution, and parallel development within these lines to a remarkable degree. I regard the testing of the second conclusion as that potentially the more fruitful for future investigations of the Cheilostomata in general. The necessary studies would involve Bryozoan workers in many fields for their completion, and observations on the following subjects would have to be made.

The form of the colony is preponderantly erect and bilaminar, but encrusting forms are known. The erect habit, with its positional dimorphism of central and marginal zooids and polymorphs, is known in several other groups, but has been insufficiently investigated. A study of these and of the early astogenetic stages may provide hitherto unrecognized patterns of colonial structure and evolution in many genera.

The occurrence of sexual polymorphs, both male and female, also with positional significance, was described and summarized for the 'Adeonidae' by Harmer (1957 : 788–821). It is also known in *Hippoporidra* (*see* Cook 1968b), and almost certainly occurs in other forms. Sexual polymorphs have probably not been recognized because the polymorphism is not necessarily reflected in the calcified parts of the individuals (*see also Hippopodinella* described by Gordon 1968), and the study of living specimens and of the lophophore and viscera has been neglected. Although sexual polymorphs have been observed and inferred in the Adeonidae and Adeonellidae, much more work, on living and preserved specimens, is needed to ascertain their detailed morphology and distribution. Preliminary examination of many fossil and Recent species has indicated that there are probably trends in the degree of differentiation of sexual polymorphs with time, which may have taxonomic and phylogenetic significance. The zooids inferred to be brooding zooids appear to be very similar in some representatives of the two families, but have not been certainly recognized in all genera. Similar kinds and degrees of polymorphism are known in other, obviously unrelated, genera, and a thorough investigation may throw light on the kind and degree of convergence which may have occurred in the Adeonidae and Adeonellidae.

Avicularia are almost invariably found throughout the two families and where present are consistently without a calcified bar. The vicarious avicularia vary from a relatively undifferentiated type, often with a frontal spiramen, to more complex individuals. Further work on their morphology and distribution, and comparison with similar types, particularly among the Anasca, would be instructive.

Electron microscopy will probably reveal considerably more evidence as to the structure and development of the calcified parts of Bryozoan colonies. It is most important that these observations are made in conjunction with those possible with a light microscope, in order that correlations may be made available for workers in the more conventional fields.

Taxonomic revisions, involving comparison of type-material with plentiful, well-preserved specimens, together with studies on population variation are urgently required, before any conclusions may be drawn as to the distribution of genera in

time and space. Finally, after extensive work on fossil and Recent populations, it may be possible to construct a hypothetical phylogenetic model for the evaluation of the evolution of the Adeonidae and Adeonellidae, and to relate them to each other and, by extrapolation, to other Cheilostome groups.

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REFERENCES

BANTA, W. C. 1970. The body wall of Cheilostome Bryozoa, III. The frontal wall of *Watersipora arcuata* Banta, with a revision of the Cryptocystidea. *J. Morph.* **135** : 37–56.

—— 1971. *Op. cit.* IV. The frontal wall of *Schizoporella unicornis* (Johnston). *Ibid.* **135** : 165–184.

BASSLER, R. S. 1953. Bryozoa. In R. C. Moore, *Treatise on Invertebrate Paleontology*, part G, **1963** : G1–G253.

BOARDMAN, R. S. & CHEETHAM, A. H. 1969. Skeletal growth, intracolony variation, and evolution in Bryozoa : a review. *J. Paleont.* **43** : 205–233.

—— & COOK, P. L. 1970. Intracolony variation and the genus concept in Bryozoa. *Proc. N. Am. Paleont. Convention* : 294–320.

BUSK, G. 1884. Report on the Polyzoa, the Cheilostomata. *Rep. Zool. Chall. Exp.* **10**, 30 : i–xxiii, 1–216.

CHEETHAM, A. H. 1968. Morphology and systematics of the Bryozoan genus *Metrarabdotos*. *Smithson. misc. Collns* **153** : 1–121.

——, RUCKER, J. B. & CARVER, R. E. 1969. Wall structure and mineralogy of the Cheilostome Bryozoan *Metrarabdotos*. *J. Paleont.* **43** : 129–135.

COOK, P. L. 1967. Polyzoa from West Africa. The Pseudostega, Cribrimorpha and some Ascophora Imperfecta. *Bull. Br. Mus. nat. Hist.* (Zool.), **15**, 7 : 321–351.

—— 1968a. Bryozoa (Polyzoa) from the coast of tropical west Africa. *Atlantide Rep.* **10** : 115–262.

—— 1968b. Observations on living Bryozoa. *Atti Soc. ital. Sci. nat.* **108** : 155–160.

GORDON, D. P. 1968. Zooidal dimorphism in the Polyzoan *Hippopodinella adpressa* (Busk). *Nature, Lond.* **219** (5154) : 633–634.

GREGORY, J. W. 1893. On the British Palaeogene Bryozoa. *Trans. zool. Soc. Lond.* **13**, 6 : 219–279.

HARMER, S. F. 1902. On the morphology of the Cheilostomata. *Q. Jl microsc. Sci.* N.S. **46** : 263–350.

—— 1957. The Polyzoa of the Siboga Expedition. Pt. 4. Cheilostomata Ascophora. *Rep. Siboga Exp.* **28d** : 641–1147.

HINCKS, T. 1887. Critical notes on the Polyzoa, pt. 1. *Ann. Mag. nat. Hist.* (5), **19**: 150–164.

JULLIEN, J. & CALVET, L. 1903. Bryozoaires provenant des compagnes de l'*Hirondelle* (1886–1888). *Rés. Camp. scient. Monaco*, **22** : 1–188.

LARWOOD, G. P. 1962. The morphology and systematics of some Cretaceous Cribrimorph Polyzoa (Pelmatoporinae). *Bull. Br. Mus. nat. Hist.* (Geol.) **6**, 1 : 1–285.

O'DONOGHUE, C. H. 1924. The Bryozoa (Polyzoa) collected by the S.S. 'Pickle'. *Rep. Fish. mar. biol. Surv. Pretoria*, **3** (1922), 10 : 1–63.

—— & DE WATTEVILLE, D. 1944. Additional notes on Bryozoa from South Africa. *Ann. Natal. Mus.* **10**, 3 : 407–432.

POWELL, N. A. 1967. Polyzoa (Bryozoa) Ascophora from North New Zealand. *Discovery Rep.* **34** : 199–394.

SILÉN, L. 1942. Origin and development of the Cheilo-ctenostomatous stem of the Bryozoa. *Zool. Bidr. Upps.* **22** : 433–488.

SMITT, F. A. 1873. Floridan Bryozoa, Pt. 2. *K. svenska VetenskAkad. Handl.* **9**, 4 : 3–84.

TAVENER SMITH, R. & WILLIAMS, A. 1970. Structure of the compensation sac in two ascophoran Bryozoans. *Proc. R. Soc.* B 175 : 235–254.

VIGNEAUX, M. 1949. Révision des Bryozoaires néogènes du Bassin d'Aquitaine. *Mém. Soc. géol. Fr.* N.S. **28**, 60 : 1–153.

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PLATE 1

Adeona sp. ? Australia, 1934.2.10.8, Busk Coll.

FIG. 1. Zooecium from near growing edge ; showing proximal and lateral frontal lamina, marginal pores and distal communication pores.

FIG. 2. Zooecium at a later ontogenetic stage ; showing fusion of distal parts of lateral laminae forming median suture, formation of secondary calcified orifice and frontal spiramen. Note early stages in formation of avicularian chamber on either side of median suture.

FIG. 3. Same zooecium as fig. 2 ; showing suture.

FIG. 4. Zooecium at a later ontogenetic stage ; showing frontal, upward extension of peristome after thickening of frontal shield, and development of avicularian chamber.

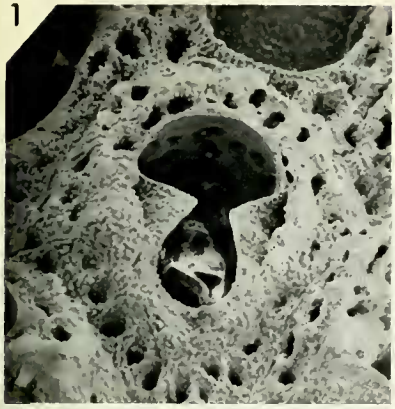
FIG. 5. Zooecium at a later ontogenetic stage ; showing formation of single avicularium proximal to secondary calcified orifice ; note apparent proximal migration of frontal spiramen.

FIG. 6. Zooecium at a later ontogenetic stage ; showing formation of avicularian rostrum and condyles.

All photographs taken using electron scanning microscope.

Magnification : Figs. 1–2, 4–6, × 145 ; fig. 3, × 370.

1



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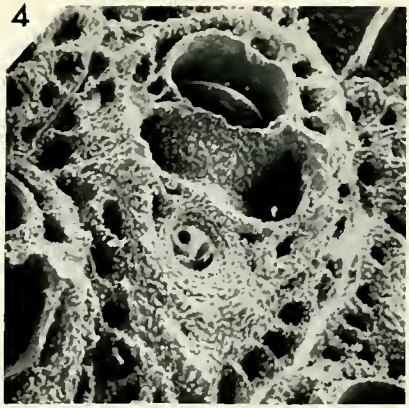

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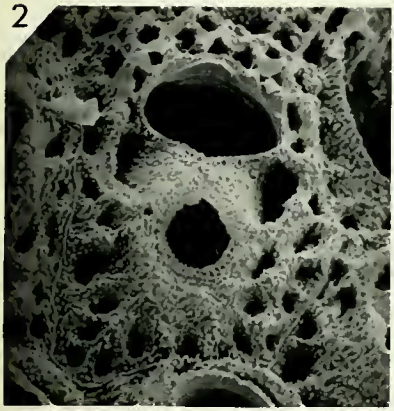

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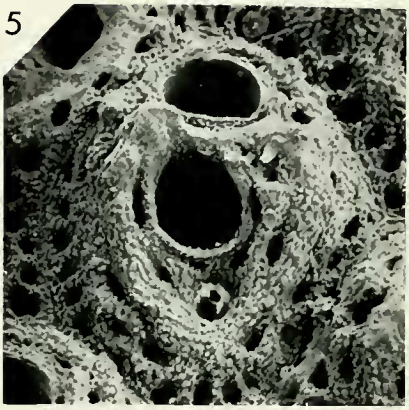

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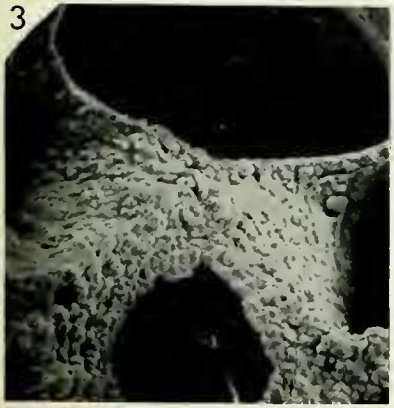

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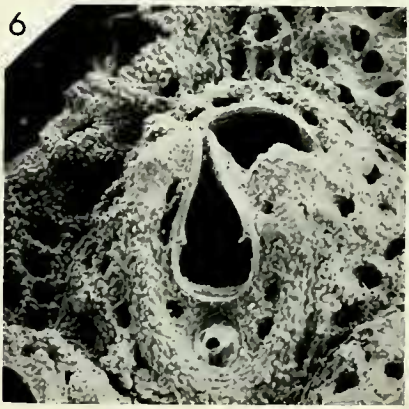


PLATE 2

Adeonellopsis and *Bracebridgia*

FIGS. 1–3. *Adeonellopsis* sp., Broughton Island, Australia, 1883.11.29.55.

FIG. 1 Zooecium near growing edge, showing primary lamina and secondary calcified orifice. Note the beginning of formation of suboral avicularian chamber and subdivision of central spiramen area into multiporous plate.

FIG 2. Same zooecium ; showing arrangement of blocks of calcification round the depressed frontal area.

FIG. 3. Same zooecium ; showing frontal spiramen. Note the smooth calcification lining the pores.

FIGS. 4–6. *Bracebridgia subsulcata* (Smitt), 28°45′ N, 85°02′ W, 30 fathoms, 'Albatross' Stn. 2405

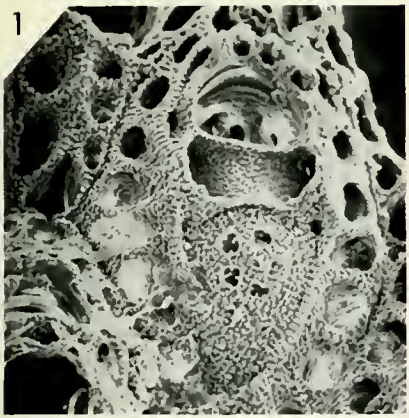
FIG. 4 Zooecium near growing edge, showing primary lamina and frontal spiramen. Note that frontal, upward extension of peristome has already taken place, and suboral avicularian chamber has begun to develop.

FIG. 5. Zooecium at a later ontogenetic stage ; showing partially occluded frontal spiramen and formation of avicularian chamber.

FIG. 6. Zooecium at much later stage ; showing frontal suboral avicularium and calcification of proximal oral process ; the peripheral ridge of frontal calcification is formed.

All photographs taken using electron scanning microscope.

Magnification : Fig. 1, × 120 ; fig. 2, × 300 ; fig. 3, × 600 ; figs. 4–6, × 140.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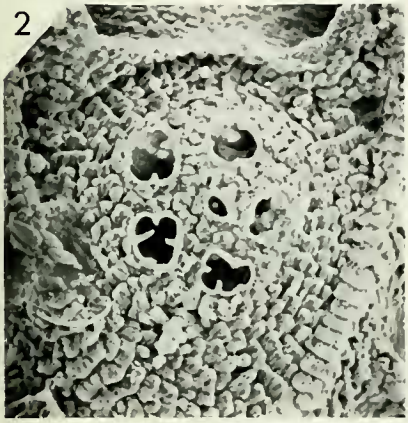
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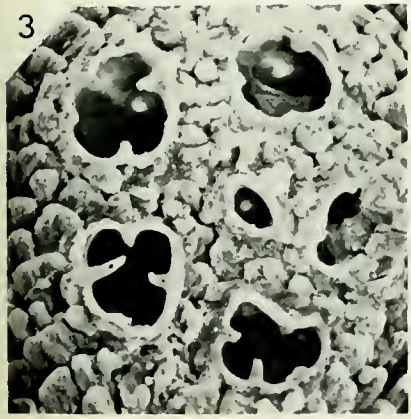
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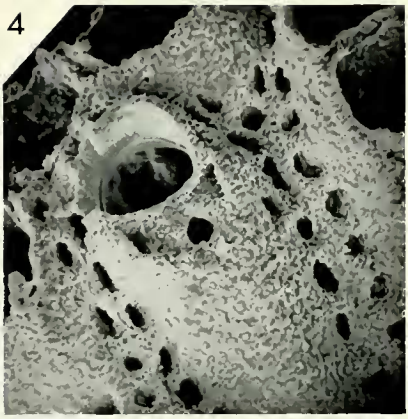
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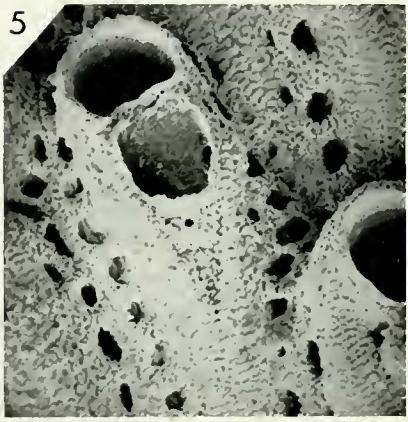
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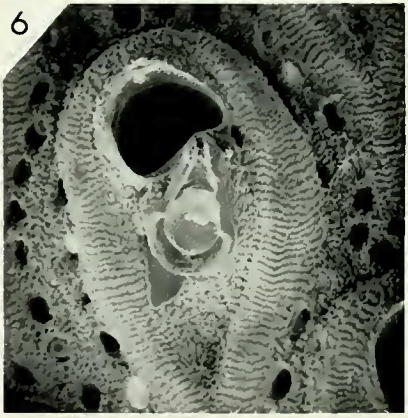
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PLATE 3

Adeonellopsis and *Adeonella*

FIGS. 1–3. *Adeonellopsis meandrina* (O'Donoghue & de Watteville), Cape of Good Hope, 1840.9.30.29, Krauss Coll.

FIG. 1. Zooecium near growing edge; showing frontal lamina at an earlier ontogenetic stage than that shown in *Adeona*, Pl. 1, fig. 1.

FIG. 2. Zooecium at a later ontogenetic stage; showing formation of frontal spiramen and secondary calcified orifice.

FIG. 3. Zooecium at a later ontogenetic stage; showing development of one of the avicularian chambers (frequently paired in this species).

FIGS. 4–6. *Adeonella coralliformis* O'Donoghue, South Africa, 1968.1.18.5, O'Donoghue Coll.

FIG. 4. Zooecium near growing edge; showing early form of primary calcified orifice, frontal pseudopores and the early formation of avicularian chambers.

FIG. 5. Zooecium at a later ontogenetic stage; showing fully formed primary calcified orifice, with complete sinus, further development of avicularian chambers, and early development of medially directed lateral peristomial processes. Note frontal, upward extension of peristome as frontal shield calcification thickens.

FIG. 6. Zooecium at a later ontogenetic stage; showing sinus of primary orifice, complete avicularian rostra, formation of supraoral bar from fusion of lateral processes, and subsequent formation of secondary calcified orifice and peristomial spiramen. Note apparent proximal migration of peristomial spiramen.

All photographs taken using electron scanning microscope.

Magnification: Figs. 1–3, × 120; figs. 4–6, × 85.

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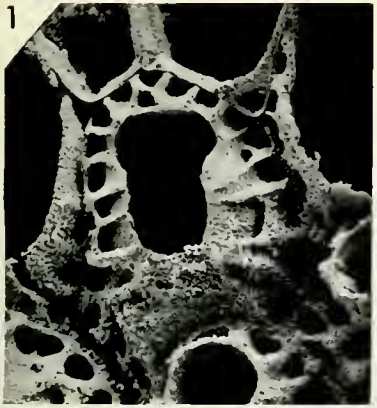

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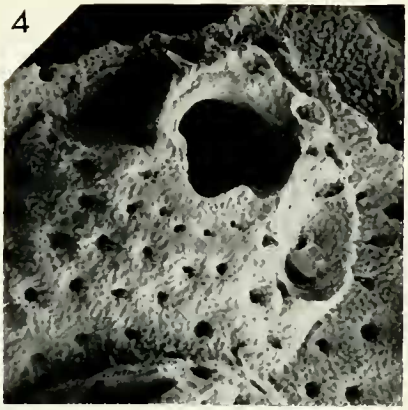

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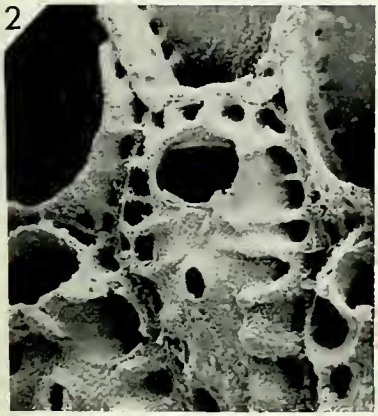

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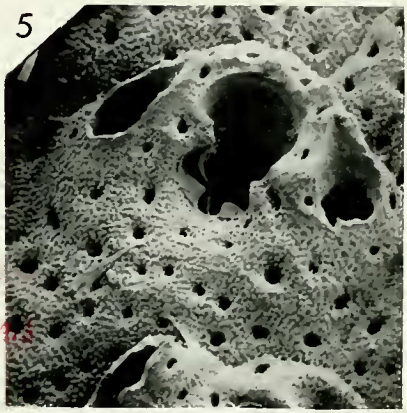

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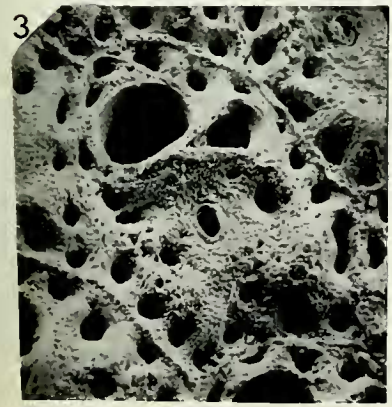
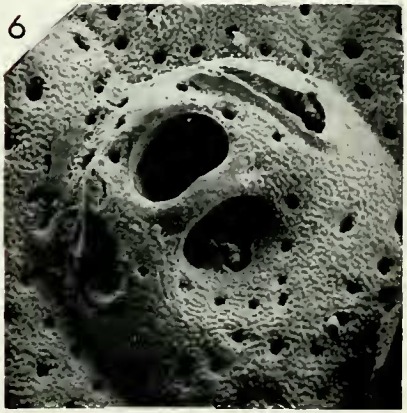
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